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Functional responses of four Sahelian tree species to resource availability☆

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ABSTRACT

Plants experience a fluctuating environment in time and space that affects resource supply. As human impacts on the environment directly and indirectly alter resource availability, it is important to address plant responses to changing resources to be able to anticipate impacts of these changes on plant communities. We analyzed plant traits to assess responses to resource limitation in four Sahelian tree species of wide ecological and socio-economic importance. We used species already adapted to harsh conditions (high temperatures, low rainfall) to anticipate how climate change could affect their growth patterns and, indirectly, their spatial distribution and the services they provide. Seedlings grew under two levels of water and nutrient additions in a factorial design. Our results showed differences among species, watering regimes, and nutrient supply in three key functional traits related to the plant's resource-use strategy, relative growth rate (RGR), root-to-shoot ratio (R/S), and specific leaf area (SLA). On average, RGR was responsive to the amount of water and nutrients, with species with high RGR showing the largest response to resource supply. RGR in the species with a conservative resource-use strategy (evergreen leaves, lowest RGR) remained unchanged with different levels of water and nutrients. Overall, large RGR was supported by large SLA. All species allocated more biomass to roots than to shoots, particularly under low resource supply, reflecting adaptive strategies to keep RGR leveled to resource supply. Not all species showed similar plasticity in their functional traits responses; however, *Acacia tortilis* and *Faidherbia albida* showed the greatest plasticity, which may explain their large geographical distribution range in Africa. Our data suggest that the different Sahelian species will respond differently to future environmental changes, likely affecting their geographical distribution, the structure of plant communities, and the services they provide.

1. Introduction

Climate alterations over the last decades may be already responsible for changes in tree species ranges (Song et al., 2016), and warming and altered precipitation patterns may profoundly alter savannas worldwide (Volder et al., 2013). Future climate projections predict severe droughts in the African savanna (Boko et al., 2007; Brooks, 2004), and the Sahel is expected to experience a combination of increased temperatures and modified precipitation regimes, which will intensify seasonal droughts (MacCracken et al., 2003; Pope et al., 2000; Wetherald and Manabe, 1995) potentially altering the function, growth, and distribution of plant functional groups (Hungate et al., 2002; Knapp et al., 2008a, b). Since drought tolerance ability is one of the strongest predictors of tree species distribution in seasonally-dry tropical environments (Box, 1995; Condit et al., 2013), understanding differences in plant adaptive responses to resource availability is important to better understand possible outcomes of these changes (Cuni-Sanchez et al., 2011; Garnier et al., 2018; Lang et al., 2018).

Seedlings are the most vulnerable stage of the plant life cycle, being particularly sensitive to water limitation during drought (Chaturvedi et al., 2013; Khurana and Singh, 2001; Montgomery and Chazdon, 2002; Padilla and Pugnaire, 2007; Yavitt and Wright, 2008). Seedling survival is strongly dependent on the severity of drought, as water stress is the main factor affecting seedling mortality in dry environments (Comita and Engelbrecht, 2009; Engelbrecht et al., 2005; Pugnaire et al., 2006; Slot and Poorter, 2007). Watering experiments in tree species of tropical moist forests also reveal that water availability controls species seasonal growth patterns and that drought stress limits seedling growth rates (Engelbrecht et al., 2006; Engelbrecht and Kursar, 2003; Paine et al., 2008; Yavitt and Wright, 2008). Hence, assessing

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seedlings responses to water availability, and how they modify their traits, will help to understand the long-term response of forest species to environmental change (Capers et al., 2005; Jump et al., 2007; Pedersen, 1998; Peñuelas et al., 2007).

Further, understanding the role of plasticity in response to resource availability will bring insights into plant growth and persistence of species in their current environments under novel conditions (Nicotra et al., 2010). While drought is acknowledged as a crucial climatic factor that would likely undermine tree survival in the future (Allen and Breshears, 1998; Hanson and Weltzin, 2000), progressive drought-induced stress is a non-linear process largely dependent on the interaction between temperature and water availability, and to plants' adaptability to higher temperatures in terms of morphology and physiology (Adams et al., 2009). The ability of plant species to cope with environmental change will depend on the capacity to adapt physiological and other functional responses to these changes; but, for an effective prediction of the capacity of populations to persist in a certain environment, empirical studies that aim to assess intra-specific response variability under controlled environmental conditions are necessary. Therefore, examination of trait variability in heterogeneous environments that reflect population-level responses to the environment can provide deeper insights into how species might respond to future environmental changes (Oke and Wang, 2015). In addition, identifying trade-offs that underlie the diversity of a species' morphology and function is important because trade-offs constrain demographic change rates and their linkages to ecosystem processes (Díaz et al., 2016; Shipley et al., 2016).

Growth rate is a prominent indicator of plant strategies that deals with environmental stress and disturbance (Pérez-Harguindeguy et al., 2013), and substantial volume of theory and data support the correspondence between functional traits and growth rate (Hunt and Cornelissen, 1997; Reich et al., 1998; Shipley, 2006). However, variation in individual-level access to resources can cause trait correlations within species to differ from inter-specific correlations (van Noordwijk and de Jong, 1986) due to phylogenetic constraints.

Here we analyzed functional responses of seedlings to simultaneous effects of moisture stress and nutrient variability in four Sahelian tree species of wide ecological and socio-economic importance. Target species were selected as representative of functional groups of the highly diverse agroforestry ecosystems in the Sahel (Diémé et al., 2018). We linked RGR and biomass allocation patterns with functional traits deemed relevant to plant persistence (Kleyer et al., 2008). We addressed responses in relative growth rate (RGR), root-to-shoot ratio (R/S) and specific leaf area (SLA) of seedlings growing under two levels of water and nutrient availability in a full factorial greenhouse experiment and explored potential trade-offs among traits. We hypothesize that 1) RGR will increase with resource supply but the magnitude of the response will depend on resource use strategies (Grime et al., 1997). We expected that 2) fast-growing species, i.e. with exploitative strategy, will show high RGR under high water and nutrient supply, but RGR will decline strongly with low resource supply levels; in contrast, 3) plants with conservative resource-use strategy will have a less plastic response to changes in water and nutrient supply, i.e., stable RGR regardless resource levels, with more biomass allocated to roots at low levels of water and nutrient supply (Meier et al., 2018). And 4) SLA, a trait strongly associated to the plant resource-use strategy, will respond in parallel to RGR.

2. Methods

A greenhouse experiment was established in 2012–2013 at the University of Almería (36° 50′ N, 2° 27′ W), Spain, using four Sahelian tree species, two dry-season deciduous species, *Acacia tortilis* (Savi) Brenan and *Adansonia digitata* L., one wet-season deciduous species (*Faidherbia albida* (Del.) Chev.), and one evergreen species, *Tamarindus indica* L. Seeds of these species were obtained in Senegal (PRONASEF, Senegal National Project of Forestry Seeds, Dakar) and subjected to a pre-germination treatment using concentrated sulfuric acid for 10 min (*T. indica*), 60 min (*A. tortilis* and *F. albida*) and 12 h (*A. digitata*). Seeds of each species were harvested in the same area so that their mother plants were subjected to the same environmental (soil and climatic) conditions. Two seeds per species were sown in a sand and vermiculite mixture (1:1 in volume) in 50 cm long, 10 cm wide PVC tubes and thinned to one after germination. Plants were watered every morning and received fertilizer (commercial NPK fertilizer [Mg-S]; 19-19-19 [2–8]) once a month between November 2012 and March 2013, just before the experiment started. In March 2013, treatments were set in a factorial design with nutrient (low and high nutrient supply) and water (low and high level of watering) as factors (2 × 2 factorial design; n = 6–9 plants per treatment and species). At the start of the experiment, plant size differed depending on the species. It was < 5 cm in *A. albida, A. digitata*, and *T. indica,* and < 15 cm in *F. albida*. Half the plants per species received a high nutrient solution (N+) of 0.5 g fertilizer per liter of water, and the other half received a low nutrient solution (N-; 0.05 g of fertilizer per liter of water). In addition, half the plants were watered once a week with 100 ml (low water supply; W-) and the other half was watered twice a week with 100 ml each time (high water supply; W+, 200 ml of water per week). So, four treatments were established according to nutrient and water regime, W + N +, W + N-, W-N+, and W-N-. Treatments were applied for four months and pots were randomly redistributed in the greenhouse once a month. Temperature within the greenhouse ranged 16–22 °C during the course of the experiment, with natural daylight length (10.5–14 hours of light).

At harvest, nine months after sowing, plants were sorted into above- and below-ground parts, and the aboveground parts were subdivided into leaves and stem. Plant parts were dried at 70 °C for 48 h and weighed. Plant traits were calculated following standard protocols (Pérez-Harguindeguy et al., 2013). In brief, six fully expanded and undamaged leaves per plant were scanned with a flatbed scanner to determine the specific leaf area (SLA; the ratio of leaf area to dry mass). Total plant biomass (TPB) was obtained by adding the dry mass of the different plant parts. Root-to-shoot ratio (R/S) was calculated by dividing root mass by shoot mass. Relative growth rate was estimated as $RGR = (\ln TPB_2 - \ln TPB_1)/(t_2 - t_1)$, where t is the elapsed time in days between sowing (t_1) and harvest (t_2). To calculate TPB_1, we selected 10 seeds per species, extracted and dried the embryos in an oven for at least 72 h at 70 °C, and weighed their dry mass with a precision balance (to 10^{-6} g). We used the mean TPB_1 value per species. We also recorded plant height (measured with a ruler to 0.1 cm).

The effect of water, soil nutrient addition on plant functional traits (RGR, SLA, R/S, biomass, plant height, allocation patterns) was analyzed with general linear models including a full-factorial design. Fixed-factors were species (as we were interested in inter-specific responses of species belonging to different functional groups), nutrient addition (low, high), watering (low, high), and the interaction across factors. Assumptions of normal distribution of residuals, homogeneity of variances were tested, met. Differences in means across treatment levels were analyzed with Fisher's least significance difference (LSD) post-hoc test. Statistical analyses were conducted in R (R Development Core Team, 2013) using the interface implemented in InfoStat-Statistical Software (Di-Rienzo et al., 2013). Reported values throughout the text, figures are means ± 1, standard error.

3. Results

There were differences in RGR, R/S and SLA among species in response to water and nutrient addition regimes (Table 1). There were significant differences in RGR among all species; RGR was greatest in *Acacia tortilis* and lowest in *Tamarindus indica* (Fig. 1). All species increased RGR with water supply (significant species × water interaction, Table 1) except *T. indica*, whose RGR remained unchanged irrespective of water and nutrient addition. Growth of the other 3 species

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Table 1
Results of linear models analysing differences in relative growth rate (RGR), root to shoot ratio (R/S) and specific leaf area (SLA) of four Sahelian tree species growing under different soil water and nutrient regimes (n = 6–9). Species, level of fertilizer or water treatments were included in the model as fixed factors with a full-factorial design. Significant p values are highlighted in bold.

	d.f.	RGR		R/S		SLA	
		F-value	p-value	F-value	p-value	F-value	p-value
(Intercept)	1	6832.59	< **0.0001**	1001.79	< **0.0001**	503.3	< **0.0001**
Species (S)	3	463.65	< **0.0001**	53.24	< **0.0001**	4.01	**0.0094**
Nutrient (N)	1	12.37	**0.0006**	7.39	**0.0076**	4.16	**0.0437**
Water (W)	1	12.34	**0.0007**	36.42	< **0.0001**	6.38	**0.0129**
S × N	3	0.47	0.7020	2.81	**0.0428**	1.78	0.1557
S × W	3	2.87	**0.0398**	8.58	< **0.0001**	0.71	0.5472
N × W	1	0.31	0.5804	8.58	< **0.0001**	0.71	0.5472
S × N × W	3	0.38	0.7709	1.2	0.3136	0.64	0.5934

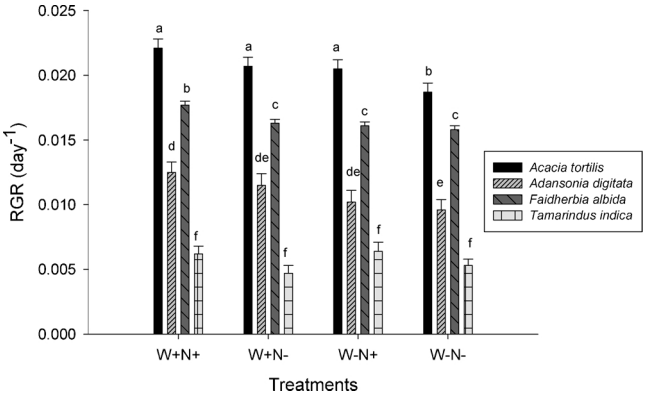

Fig. 1. Relative growth rate (RGR) of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N + and low, N-) and two water regimes (W + and W-). Data are mean ± 1SE (n = 6–9). Different letters show significant differences among species and treatments (post-hoc comparisons among species × water × nutrient levels).

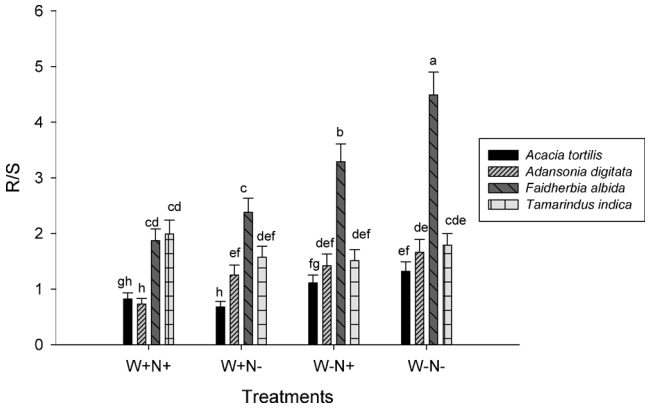

Fig. 3. Root shoot ratio (R/S) of *Acacia tortilis*, *Adansonia digitata*, *Faidherbia albida* and *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N + and low, N-) and two water regimes (W + and W-). Data are mean ± 1SE (n = 6–9). Different letters show significant differences (post-hoc comparisons among species × water × nutrient levels).

reacted similarly to both water and nutrient availability, and RGR in the two extreme treatments (W+N+ *vs.* W-N-) were always different (higher with higher resource supply) regardless of species. RGR response at intermediate resource supply (W+N- or W-N+) was in between above extreme treatments (Fig. 1).

SLA varied among species as well (Table 1), being greatest in *Adansonia digitata* (Fig. 2). SLA responded similarly to the addition of nutrient and water in all species; i.e., there were no significant

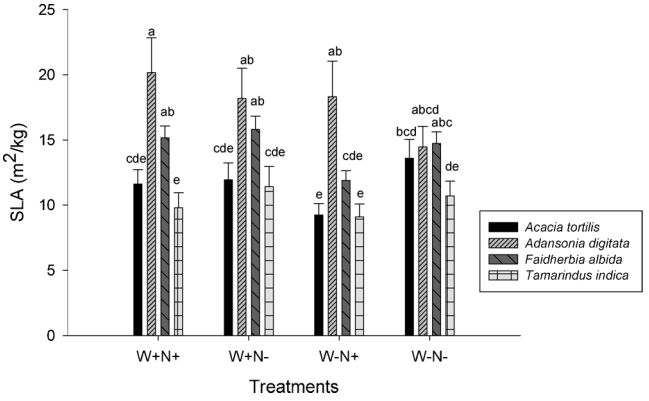

Fig. 2. Specific leaf area (SLA) of *Acacia tortilis*, *Adansonia digitata*, *Faidherbia albida* and *Tamarindus indica* individuals growing at two levels of nutrient availability (high, N + and low, N-) and two water regimes (W + and W-). Data are mean ± 1SE (n = 6–9). Different letters show significant differences (post-hoc comparisons among species × water × nutrient levels).

interaction Species × N; Species × W or Species × N × W (Table 1).

All species had, on average, R/S values above 1 (Fig. 3), meaning they allocated more biomass to roots than to aboveground parts (Fig. 4). There were significant differences in R/S among species, and R/S allocation responded also to the nutrient and water levels (Table 1). R/S generally increased as resources became limiting (Fig. 3), and the significant interaction N × W indicated that allocation to roots or shoots responded non-additively to nutrient and water levels (i.e., significantly lower and higher responses than average in W-N- and W+N + treatments). At the same time, R/S responses to nutrient and water levels depended on the species (significant interaction S × N and S × W; Table 1). The highest differences in R/S response to the treatments was observed in *F. albida,* whereas R/S in *T. indicus* remained unchanged regardless of the treatment (Fig. 3). Overall, *A. tortilis* and *F. albida* were the most responsive species to differences in water supply (i.e., differences in R/S were greatest between W- and W+ treatments). However, R/S values are size-dependent and therefore change with plant size. To check whether it was the case we compared the slopes of ln root vs ln shoot among treatments within a species (Fig. A1). We found that there was true plasticity (*sensu* e.g., Weiner, 2004) only in *Adansonia digitata*, but *Faidherbia albida* showed plasticity with respect to watering treatments.

Nutrient levels affected different morphological traits (Table 2). Plants in the high nutrient treatment were taller and had higher shoot and leaf mass than plants in the low nutrient treatment except *T. indica*, but there was no effect of nutrient regime on root mass of the different species (Table 2). Hence, plant size in general was much larger in the high-nutrient treatment (Table 2) except for *T. indica*. Water also had a significant effect on plant size. Low water availability decreased overall

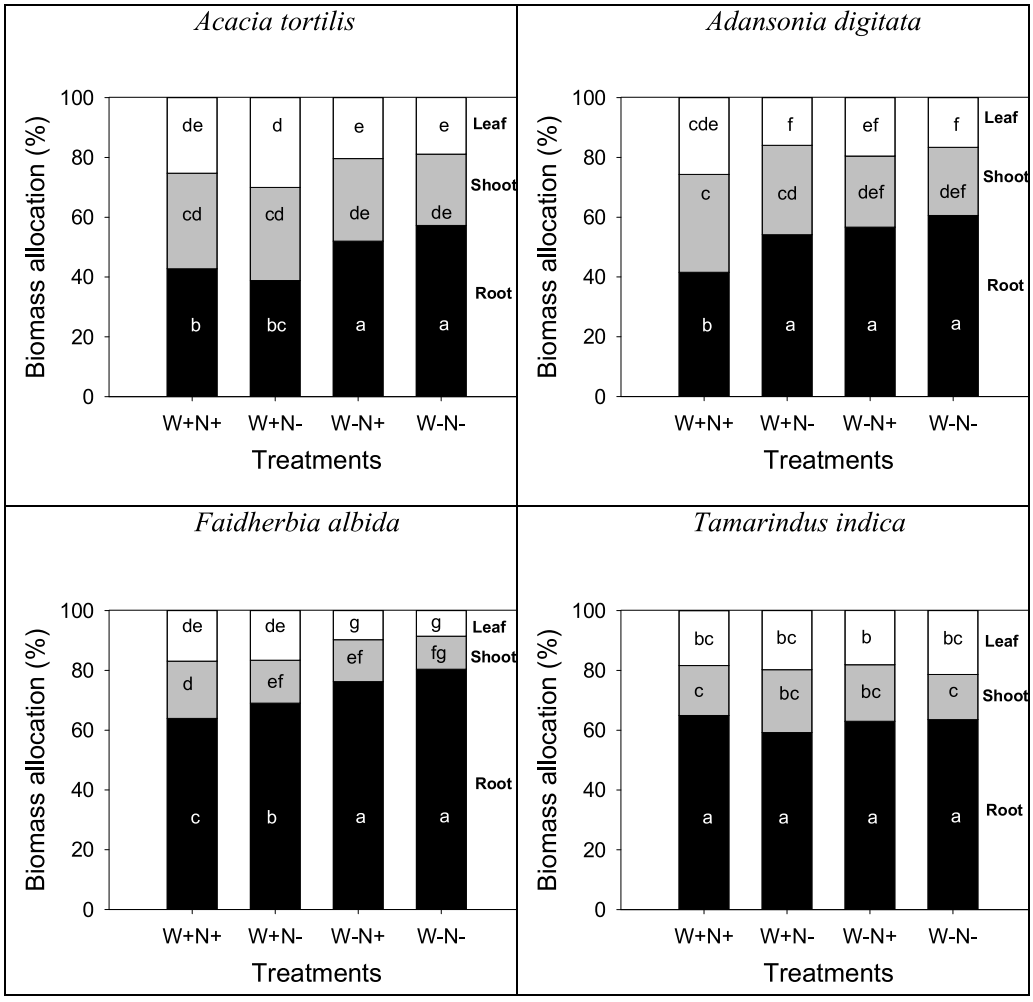

Fig. 4. Mean relative biomass allocation (%) to roots, shoots and leaves of *Acacia tortilis, Adansonia digitata, Faidherbia albida* and *Tamarindus indica* plants grown at two levels of nutrient availability (high: N+, and low: N-) and two water regimes (W + and W-). Different letters show significant differences in biomass allocation across plant organs and treatments for each species separately (post-hoc comparisons among plant organs × water × nutrient levels).

plant height and mass (Table 3). Total plant mass was much higher in the high-water regime (Table 3), except in *A. digitata* and *T. indica*. Overall, *T. indica* was the only species that did not show a significant response regarding biomass or allocation patterns in response to nutrient or water addition (Fig. 4).

4. Discussion

The four Sahelian tree species in our study differed significantly in RGR, and as expected, plant size and growth rate responded positively and consistently to both nutrient and water levels (Cornelissen et al., 1998), although the response to water levels was species-specific (significant interaction S × W). RGR was significantly higher when both resources were high compared to low, in agreement with published reports (e.g., Poorter et al., 1989). In general, species maintained a RGR ranking across resource availability levels, i.e., *A. tortilis, F. albida, A. digitata* and *T. indica* showed highest to lowest RGRs regardless of resource supply. *Acacia tortilis* maintained high RGR under all treatments except with the lowest levels of nutrient and water supply, while RGR in *T. indica* remained unchanged notwithstanding nutrient and water levels. These results support our prediction of a larger plasticity in response to varying levels of water and nutrient supply in species with high RGR (resource exploitative strategy) and low plastic capacity in species with low RGR (conservative resource strategy). Our results are also indicative that maintaining an optimal RGR (i.e., adjusted to environmental conditions) seems to be an important plant strategy

Table 2
Responses of our four target tree species to nutrient addition. Data are mean ± 1SE (n = 6–9); different letters in a row show significant differences between species ($p < 0.05$).

	Acacia tortilis		Adansonia digitata		Faidherbia albida		Tamarindus indica	
	High	Low	High	Low	High	Low	High	Low
Shoot mass (g)	1.61 ± 0.22^{a}	0.73 ± 0.06^{b}	1.34 ± 0.23^{a}	0.55 ± 0.05^{c}	1.22 ± 0.12^{a}	0.66 ± 0.04^{bc}	0.19 ± 0.02^{d}	0.18 ± 0.02^{d}
Root mass (g)	2.17 ± 0.3^{b}	1.60 ± 0.19^{b}	2.12 ± 0.42^{b}	1.46 ± 0.21^{b}	4.58 ± 0.29^{a}	4.18 ± 0.27^{a}	0.71 ± 0.09^{c}	0.76 ± 0.09^{c}
Leaf mass (g)	1.27 ± 0.14^{a}	0.56 ± 0.05^{bc}	0.97 ± 0.25^{ab}	0.44 ± 0.06^{c}	1.19 ± 0.13^{a}	0.47 ± 0.04^{c}	0.22 ± 0.03^{d}	0.26 ± 0.03^{d}
Total plant mass (g)	5.05 ± 0.56^{b}	2.86 ± 0.26^{cd}	4.44 ± 0.76^{bc}	2.44 ± 0.32^{d}	6.99 ± 0.47^{a}	5.30 ± 0.31^{b}	1.12 ± 0.13^{e}	1.20 ± 0.13^{e}
Plant height (cm)	44.67 ± 3.16^{a}	29.97 ± 1.70^{c}	24.45 ± 2.85^{c}	14.62 ± 1.43^{d}	46.96 ± 2.33^{a}	35.55 ± 1.57^{b}	10.22 ± 0.78^{e}	9.23 ± 0.74^{e}

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Table 3
Responses of our four target tree species to water addition. Data are mean ± 1SE (n = 6–9); different letters in a row show significant differences between species ($p < 0.05$).

	Acacia tortilis		Adansonia digitata		Faidherbia albida		Tamarindus indica	
	High	Low	High	Low	High	Low	High	Low
Shoot mass (g/plant)	1.44 ± 0.21^{a}	0.89 ± 0.09^{b}	1.15 ± 0.22^{ab}	0.74 ± 0.09^{bc}	1.19 ± 0.12^{a}	0.69 ± 0.05^{c}	0.21 ± 0.02^{d}	0.16 ± 0.02^{d}
Root mass (g/plant)	2.18 ± 0.30^{b}	1.58 ± 0.20^{b}	1.79 ± 0.30^{b}	1.79 ± 0.36^{b}	4.73 ± 0.30^{a}	4.03 ± 0.26^{a}	0.82 ± 0.10^{c}	0.65 ± 0.09^{c}
Leaf mass (g/plant)	1.07 ± 0.12^{a}	0.76 ± 0.08^{bc}	0.92 ± 0.25^{ab}	0.49 ± 0.07^{d}	0.98 ± 0.12^{ab}	0.68 ± 0.06^{c}	0.26 ± 0.04^{d}	0.22 ± 0.03^{d}
Total plant mass (g/plant)	4.70 ± 0.52^{bc}	3.21 ± 0.32^{d}	3.86 ± 0.67^{cd}	3.02 ± 0.47^{d}	6.90 ± 0.47^{a}	5.40 ± 0.31^{b}	1.29 ± 0.14^{e}	1.04 ± 0.12^{e}
Plant height (cm)	38.14 ± 2.4^{b}	36.49 ± 2.67^{b}	22.86 ± 2.73^{c}	16.21 ± 1.66^{d}	45.33 ± 2.26^{a}	37.17 ± 1.68^{b}	10.16 ± 0.8^{e}	9.29 ± 0.71^{e}

irrespective of resource supply, since a high RGR is critical for plants to grow and occupy space, both below- and above-ground, to get a larger share of resources (Grime, 1998; Ruiz-Robleto and Villar, 2005). All species except *T. indica* are deciduous species and show RGR values between 0.005 and 0.023 g g^{-1} d^{-1}, which is a rather high range compared to tree species from other dry environments (Atta et al., 2012; Hoffmann and Franco, 2003; Lamers et al., 2006). Overall, species with high RGR generally have high rates of photosynthesis and respiration per unit mass, requiring high nutrient levels to sustain such physiological activity and high leaf turnover. Slow-growing species show opposite patterns (Reich et al., 1997; Wright et al., 2004). In contrast to the deciduous species in our study, the evergreen *T. indica* did not respond to resource addition. It is a slow-growing species (Diallo et al., 2008; El-Siddig et al., 2006) native to dry, subtropical environments and may have, over evolutionary time, adjusted a low resource demand to a low supply to avoid exhausting limiting resources. This way the low RGR is closer to its optimum (Chapin, 1980; Grime and Hunt, 1975). The lack of a stronger response of species with a resource exploitative strategy to resource shortage indicates the presence of trade-offs between traits and with biophysical constraints that result in convergence of resource acquisition strategies (Reich, 2014).

The RGR is a product of net assimilation rate (NAR) and leaf area ratio (LAR) (Evans, 1972). LAR in turn can be partitioned into specific leaf area (SLA) and leaf mass ratio (LMR), or the dry mass of leaves relative to total plant dry mass. Most studies show that LAR is the factor that best explains differences in RGR, and the most important component of LAR is SLA (Antúnez et al., 2001; Hoffmann and Franco, 2003; Ruiz-Robleto and Villar, 2005) further reflecting a trade-off in plant resource-use strategy tightly coupled to resource availability (Grime et al., 1997). In our experiment, SLA differed among species and across water and nutrient supply levels (Coley et al., 1985; Evans, 1972; Lavorel and Garnier, 2002). Therefore, changes in RGR mostly paralleled variations in SLA, suggesting that SLA was a key factor sustaining RGR (Poorter and Garnier, 2007).

Biomass allocation patterns vary among species and are sensitive to environmental clues (Atkin et al., 2006). Many reports have shown that drought influences allocation patterns (Ledo et al., 2018; Liu and Stützel, 2004; Poorter et al., 2015; Spollen et al., 1993) particularly R/S values (Poorter et al., 2012; Turner, 1997). Plants with a higher allocation to roots can compete more effectively for soil resources while those with a higher proportion of shoots can collect more radiation (Bloom et al., 1985; Tilman, 1988). In our experiment, R/S values were generally well above 1 irrespective of the species, suggesting a genetically-fixed higher biomass allocation to roots in seedlings of species adapted to infertile environments (Aerts and Chapin, 2000; Chapin, 1980; Lambers et al., 2008) or with severe water shortage (Fernández and Reynolds, 2000; Lambers et al., 2008; Padilla et al., 2009; Wright and Westoby, 1999). Since seedling growth rate is an important life history trait, critical for plant survival and establishment in water-limited environments, we expect traits in early ontogenetic stages to contribute significantly to the species' adaptive capacity. It is worth to note that R/S changes with plant development, as seedlings allocate more biomass to roots (Gedroc et al., 1996), and therefore our results may be consequence of differences in plant size (Husáková et al., 2018). In our dataset, however, there was true plasticity (*sensu* Weiner, 2004) in *Adansonia digitata*, while *Faidherbia albida* showed plasticity with respect to watering treatments. Therefore, we can say that, for these species, the differential allocation to roots can be interpreted as a strategy response to water limitation (Ledo et al., 2018). R/S was highest in *F. albida*, reaching a value of 4 under low water and nutrient levels and reflecting its ability to strongly alter allocation patterns. In fact, *F. albida* is a species very sensitive to drought (Roupsard, 1997) and its ability to quickly reach deeper, moist soil horizons may be critical in coping with drought at such an early stage, as has been shown for other woody species in dry conditions (Padilla and Pugnaire, 2007). Opposite to its dramatic response concerning R/S, RGR did not change much in *F. albida*, and SLA tended to decrease only under reduced water, but high N availability.

In our experiment, R/S in baobab *(A. digitata)* responded to N addition but only when water was available. This may be because, while adult baobab trees accumulate water in their stem, baobab seedlings use the taproot as main storage organ (Wickens and Lowe, 2008) allocating more resources to belowground structures than adults (Cuni-Sanchez et al., 2011), particularly when water is limiting. A similar strategy has also been observed in other tropical tree species (Poorter and Markesteijn, 2008). Given the importance of the taproot for seedling survival under dry spells (Padilla and Pugnaire, 2007; Poorter and Markesteijn, 2008), seedlings with relatively larger taproots have a higher chance of survival in drought-prone environments than seedlings with relatively smaller taproots, because they can store more water and carbohydrates (Kabeya and Sakai, 2003) and keep the root in contact with moist soil horizons (Padilla and Pugnaire, 2007).

A characteristic of plants in arid environments such as the Sahelian savanna is to show high temporal and spatial variation in growth patterns, which depends on environmental variability, particularly soil moisture (Abdelrahman and Krzywinski, 2008). Leaf habit, i.e. whether a species is evergreen or deciduous, has been linked to divergent plant strategies in seasonal climates (Markesteijn and Poorter, 2009; Tomlinson et al., 2012) as the Sahel. Deciduous species may allocate more resources to roots than evergreen species in any seasonal environment, defining distinct biomass partitioning patterns between leaf habits (Espelta et al., 2005). Within our species, *F. albida* and *A. tortilis* showed high plasticity in their functional traits responses allowing them to cope with water and nutrient variability, which may be a reason behind their large geographical spread in Africa, as they are able to cope with contrasted supply levels of water and nutrients.

5. Conclusions

Our data show that important plant functional traits changed strongly in response to changing resource availability, and that higher RGR was supported by larger SLA. Overall, seedlings of the Sahelian species in our study allocated more biomass to roots than to shoots, reaching 4-fold at times, reflecting adaptive strategies to keep RGR leveled to resource supply. Overall, functional traits other than R/S responded more to nutrient than to water addition, and two species, *A.*

tortilis and *F. albida*, showed high phenotypic plasticity, which may underlie their large distribution area. Our data suggest that the different Sahelian species will respond differently to future environmental changes, which will likely affect their geographic distribution and therefore the structure of the plant communities they are part of.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.flora.2018.10.009.

References

Abdelrahman, H.F., Krzywinski, K., 2008. Environmental effects on morphology of *Acacia tortilis* group in the Red Sea Hills, north-eastern Sudan and South-Eastern Egypt. For. Ecol. Manage. 255, 254–263.

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. U. S. A. 106, 7063–7066.

Aerts, R., Chapin, F.S.I.I.I., 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv. Ecol. Res. 30, 1–67.

Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. Proc. Natl. Acad. Sci. U. S. A. 95, 14839–14842.

Antúnez, I., Retamosa, E.C., Villar, R., 2001. Relative growth rate in phylogenetically related deciduous and evergreen woody species. Oecologia 128, 172–180.

Atkin, O.K., Loveys, B.R., Atkinson, L.J., Pons, T.L., 2006. Phenotypic plasticity and growth temperature: understanding interspecific variability. J. Exp. Bot. 57, 267–281.

Atta, H.A.E., Aref, I.M., Ahmed, A.I., Khan, P.R., 2012. Morphological and anatomical response of *Acacia ehrenbergiana* Hayne and *Acacia tortilis* (Forssk) Haynes subspp. *Raddiana* seedlings to induced water stress. African J. Biotechnol. 11, 10188–10199.

Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants – an economic analogy. Annu. Rev. Ecol. Evol. Syst. 16, 363–392.

Boko, M., Niang, I., Nyong, A., Vogel, C., Githeko, A., Medany, M., Osman-Elasha, B., Tabo, R., Yanda, P., 2007. Africa. In: Parry, M., Canziani, J., Palutikof, J., Linden, Pj, Hanson, C. (Eds.), Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 433–467.

Box, E.O., 1995. Factors determining distributions of tree species and plant functional types. Vegetatio 121, 101–116.

Brooks, N., 2004. Drought in the African Sahel: Long Term Perspectives and Future Prospects. Norwich, UK. .

Capers, R.S., Chazdon, R.L., Brenes, A.R., Alvarado, B.V., 2005. Successional dynamics of woody seedling communities in wet tropical secondary forests. J. Ecol. 93, 1071–1084.

Chapin III., F.S., 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11, 233–260.

Chaturvedi, R.K., Raghubanshi, A.S., Singh, J.S., 2013. Growth of tree seedlings in a tropical dry forest in relation to soil moisture and leaf traits. J. Plant Ecol. 6, 158–170.

Coley, P.D., Bryant, J.P., Chapin, F.S.I.I.I., 1985. Resource availability and plant anti-herbivore defense. Science 230, 895–899.

Comita, L.S., Engelbrecht, B.M.J., 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90, 2755–2765.

Condit, R., Engelbrecht, B.M.J., Pino, D., Perez, R., Turner, B.L., 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proc. Natl. Acad. Sci. U. S. A. 110, 5064–5068.

Cornelissen, J.H., Castro-Díez, P., Carnelli, A.L., 1998. Variation in relative growth rate among woody species. In: Lambers, H., Poorter, H., Van-Vuuren, M. (Eds.), Inherent Variation in Plant Growth Physiological Mechanisms and Ecological Consequences. Backhuys Publishers, Leiden, pp. 363–392.

Cuni-Sanchez, A., Smedt, S.D., Haq, N., Samson, R., 2011. Variation in baobab seedling morphology and its implications for selecting superior planting material. Sci. Hortic. (Amsterdam) 130, 109–117.

Di-Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M., Robledo, C.W., 2013. InfoStat.InfoStat.

Diallo, B., Mckey, D., Chevallier, M.H., Joly, H., Hossaert-Mckey, M., 2008. Breeding system and pollination biology of the semi-domesticated fruit tree, *Tamarindus indica* L., (Leguminosae: caesalpinioideae): implications for fruit production, selective breeding, and conservation of genetic resources. African J. Biotechnol. 7, 4068–4075.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171.

Diémé, J.S., Diouf, M., Armas, C., Rusch, G.M., Pugnaire, F.I., 2018. Functional groups of Sahelian trees in a semiarid agroforestry system of Senegal. J. Plant Ecol. 11, 375–384.

El-Siddig, K., Gunasena, H., Prasad, B., Pushpakumara, D., Ramana, K., Vijayand, P., Williams, J., 2006. Tamarind (*Tamarindus indica* L.). Southampton Centre for Underutilsed Crops, Southampton, UK.

Engelbrecht, B.M.J., Kursar, T.A., 2003. Comparative drought-resistance of seedlings of 28 species co-occuring tropical woody plants. Oecologia 136, 383–393.

Engelbrecht, B.M., Kursar, T.A., Tyree, M.T., 2005. Drought effects on seedling survival in a tropical moist forest. Trees 19, 312–321.

Engelbrecht, B.M.J., Dalling, J.W., Pearson, T.R.H., Wolf, R.L., Galvez, D.A., Koehler, T., Tyree, M.T., Kursar, T.A., 2006. Short dry spells in the wet season increase mortality of tropical pioneer seedlings. Oecologia 148, 258–269.

Espelta, J.M., Cortés, P., Mangirón, M., Retana, J., 2005. Differences in biomass partitioning, leaf nitrogen content, and water use efficiency ($\delta^{13}C$) result in similar performance of seedlings of two Mediterranean oaks with contrasting leaf habit. Ecoscience 12, 447–454.

Evans, G.C., 1972. The Quantitative Analysis of Plant Growth. Blackwell Scientific Publications, Oxford, UK.

Fernández, R.J., Reynolds, J.F., 2000. Potential growth and drought tolerance of eight desert grasses: lack of a tradeoff? Oecologia 123, 90–98.

Garnier, E., Vile, D., Roumet, C., Lavorel, S., Grigulis, K., Navas, M.L., Lloret, F., 2018. Inter- and intra-specific trait shifts in sites differing in aridity at the north western edge of the Mediterranean Biogeographic Region (in press). Flora. https://doi.org/10.1016/j.flora.2018.07.009.

Gedroc, J.J., McConnaughay, K.D.M., Coleman, J.S., 1996. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? Funct. Ecol. 10, 44–50.

Grime, J.P., 1998. Benefits of biodiversity effects on ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.

Grime, J.P., Hunt, R., 1975. Relative growth-rate: its range and adaptive significance in a local flora. J. Ecol. 63, 393–422.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C., Whitehouse, J., 1997. Integrated screening validates primary axis of specialisation in plants. Oikos 79, 259–281.

Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. Sci. Total Environ. 262, 205–220.

Hoffmann, W.A., Franco, A.C., 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. J. Ecol. 91, 475–484.

Hungate, B., Reichstein, M., Dijkstra, P., Johnson, D., Hymus, G., Tenhunen, J.D., Hinkle, C.R., Drake, B., 2002. Evapotranspiration and soil water content in a scrub-oak woodland under carbon dioxide enrichment. Glob. Change Biol. 8, 289–298.

Hunt, R., Cornelissen, J.H.C., 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytol. 135, 395–417.

Husáková, I., Weiner, J., Münzbergová, Z., 2018. Species traits and shoot–root biomass allocation in 20 dry-grassland species. J. Plant Ecol. 11, 273–285.

Jump, A.S., Hunt, J.M., Penuelas, J., 2007. Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. Ecoscience 14, 507–518.

Kabeya, D., Sakai, S., 2003. The role of roots and cotyledons as storage organs in early stages of establishment in *Quercus crispula*: a quantitative analysis of the non-structural carbohydrate in cotyledons and roots. Ann. Bot. 92, 537–545.

Khurana, E., Singh, J.S., 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environ. Conserv. 28, 39–52.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Groenendael, J.M., van, Klimes, L., Klimesova, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Gotzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J. Ecol. 96, 1266–1274.

Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., Smith, M.D., Smith, S.D., Bell, J.E., Fay, P.A., Heisler, J.L., Leavitt, S.W., Sherry, R., Smith, B., Weng, E., 2008a. Consequences of more extreme precipitation regimes for terrestrial ecosystems. Aibs Bull. 58, 811–821.

Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, M.S., Ewers, B.E., Peters,

D.P., Young, D.R., Shaver, G.R., Pendall, E., Cleary, M.B., 2008b. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Glob. Change Biol. 14, 615–623.
Lambers, H., Chapin, F.S., Pons, T.L., 2008. Plant Physiological Ecology, 2nd ed. Springer.
Lamers, J.P.A., Khamzina, A., Worbes, M., 2006. The analyses of physiological and morphological attributes of 10 tree species for early determination of their suitability to afforest degraded landscapes in the Aral Sea Basin of Uzbekistan. For. Ecol. Manage. 221, 249–259.
Lang, B., Geiger, A., Oyunbileg, M., Ahlborn, J., von Wehrden, H., Wesche, K., Oyuntsetseg, B., Römermann, C., 2018. Intraspecific trait variation patterns along a precipitation gradient in Mongolian rangelands (in press). Flora.
Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem function from plant traits: revisiting the holy grail. Funct. Ecol. 16, 545–556.
Ledo, A., et al., 2018. Tree size and climatic water deficit control root to shoot ratio in individual trees globally. New Phytol. 217, 8–11.
Liu, F., Stützel, H., 2004. Biomass partitioning, specific leaf area, and water use efficiency of vegetable amaranth (*Amaranthus spp.)* in response to drought stress. Sci. Hortic. (Amsterdam) 102, 15–27.
MacCracken, M.C., Barron, E.J., Easterling, D.R., Felzer, B.S., Karl, T.R., 2003. Climate change scenarios for the US national assessment. Bull. Am. Meteorol. Soc. 84, 1711–1723.
Markesteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. J. Ecol. 97, 311–325.
Meier, I.C., Knutzen, F., Eder, L.M., Müller-Haubold, H., Goebel, M.-O., Bachmann, J., Hertel, D., Leuschner, C., 2018. The deep root system of *Fagus sylvatica* on sandy soil: structure and variation across a precipitation gradient. Ecosystems 21, 280–296.
Montgomery, R.A., Chazdon, R.L., 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. Oecologia 131, 165–174.
Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, P.P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends Plant Sci. 15, 684–692.
Oke, T.A., Wang, J.R., 2015. Assessing population-level response to interacting temperature and moisture stress. Ecol. Res. 30, 931–940.
Padilla, F.M., Pugnaire, F.I., 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Funct. Ecol. 21, 489–495.
Padilla, F.M., Miranda, J.D., Jorquera, M.J., Pugnaire, F.I., 2009. Variability in amount and frequency of water supply affects roots but not growth of arid shrubs. Plant Ecol. 204, 261–270.
Paine, C.E.T., Harms, K.E., Ramos, J., 2008. Supplemental irrigation increases seedling performance and diversity in a tropical forest. J. Trop. Ecol. 25, 171–180.
Pedersen, B.S., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. Ecology 79, 79–93.
Peñuelas, J., Ogaya, R., Boada, M., Jump, S.A., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia, NE Spain. Ecography 30, 829–837.
Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S.C., Ornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C.D., Buchmann, N., Funes, G., Quetier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H.T., Heijden, M.G.A.V.D., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234.
Poorter, H., 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In: Lambers, H., Cambridge, M.L., Konings, H., Pons, T.L. (Eds.), Causes and Consequences of Variation in Growth Rate and Productivity in Plants. SPB Academic Publishing, The Hague, The Netherlands, pp. 101–123.
Poorter, H., Garnier, E., 2007. Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire, F.I., Valladares, F. (Eds.), Handbook of Functional Plant Ecology. CRC Press, Boca Raton, Florida, pp. 82–114.
Poorter, H., Jagodzinski, A.M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., Usoltsev, V.A., Buckley, T.N., Reich, P.B., Sack, L., 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. New Phytol. 208, 736–749.
Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol. 193, 30–50.
Poorter, L., Markesteijn, L., 2008. Seedling traits determine drought tolerance of tropical tree species. Biotropica 40, 321–331.
Pope, V.D., Gallani, M.L., Rowntree, P.R., Stratton, R.A., 2000. The impact of new physical parametrizations in the Hadley Centre climate model: HadAM3. Clim. Dyn. 16, 123–146.
Pugnaire, F.I., Luque, M.T., Armas, C., Gutiérrez, L., 2006. Colonization processes in semi-arid Mediterranean old-fields. J. Arid Environ. 65, 591–603.
R Development Core Team, 2013. R: A Language and Environment for Statistical Computing.
Reich, P.B., 2014. The world-wide "fast-slow" plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301.
Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W., Buschena, C., 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Funct. Ecol. 12, 327–338.
Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: global convergence in plant functioning. Proc. Natl. Acad. Sci. U. S. A. 94, 13730–13734.
Roupsard, O., 1997. Écophysiologie Et Diversité Génétique De *Faidherbia albida* (Del.) A. Chev. (syn. *Acacia albida* Del.), Un Arbre à Usages Multiples d'Afrique Semi-aride. Fonctionnement Hydrique Et Efficience d'utilisation De l'eau d'arbres Adultes En Parc Agroforestier Et Des Juvéniles En Conditions Contrôlées. PhD Thesis. Université H Poincaré de, Nancy I, France.
Ruiz-Robleto, J., Villar, R., 2005. Relative growth rate and biomass allocation in ten woody species with different leaf longevity using phylogenetic independent contrasts (PICs). Plant Biol. 7, 484–494.
Shipley, B., 2006. Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. Funct. Ecol. 20, 565–574.
Shipley, B., De Bello, F., Cornelissen, J.H.C., Laliberté, E., Laughlin, D.C., Reich, P.B., 2016. Reinforcing loose foundation stones in trait-based plant ecology. Oecologia 180, 923–931.
Slot, M., Poorter, L., 2007. Diversity of tropical tree seedling responses to drought. Biotropica 39, 683–690.
Song, X., Li, J., Zhang, W., Tang, Y., Sun, Z., Cao, M., 2016. Variant responses of tree seedling to seasonal drought stress along an elevational transect in tropical montane forests. Sci. Rep. 6, 36438.
Spollen, W.G., Sharp, R.E., Saab, I.N., Wu, Y., 1993. Regulation of cell expansion in roots and shoots at low water potentials. In: Smith, J.A.C., Griffiths, H. (Eds.), Water Deficits, Plant Responses from Cell to Community. Bios Scientific Publishers Oxford, pp. 37–52.
Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton.
Tomlinson, K.W., Sterck, F.J., Bongers, F., da Silva, D.A., Barbosa, E.R.M., Ward, D., Bakker, F.T., van Kaauwen, M., Prins, H.H.T., de Bie, S., van Langevelde, F., 2012. Biomass partitioning and root morphology of savanna trees across a water gradient. J. Ecol. 100, 1113–1121.
Turner, N.C., 1997. Further progress in crop water relations. Adv. Agron. 58, 293–338.
van Noordwijk, A.J., de Jong, G., 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. 128, 137–142.
Volder, A., Briske, D.D., Tjoelker, M.G., 2013. Climate warming and precipitation redistribution modify tree–grass interactions and tree species establishment in a warm-temperate savannah. Glob. Chang. Biol. 19, 843–857.
Weiner, J., 2004. Allocation, plasticity and allometry in plants. Perspect. Plant Ecol. Evol. Syst. 6, 207–215.
Wetherald, R.T., Manabe, S., 1995. The mechanisms of summer dryness induced by greenhouse warming. J. Clim. 8, 3096–3108.
Wickens, G.E., Lowe, P., 2008. The Baobabs: Pachycauls of Africa, Madagascar and Australia. Springer, London, UK.
Wright, I.J., Westoby, M., 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. J. Ecol. 87, 85–97.
Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.
Yavitt, J.B., Wright, S.J., 2008. Seedling growth responses to water and nutrient augmentation in the understory of a lowland moist forest, Panama. J. Trop. Ecol. 24, 19–26.